EFFECTS OF SUBZERO TEMPERATURES UPON POPULATIONS OF THE WESTERN PINE BEETLE, DENDROCTONUS BREVICOMIS LEC.

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BRIEF ABSTRACT

Field observations of the effects of subzero temperatures upon western pine beetle broods during the winters of 1932-33 and 1935-36 showed mortalities as high as 85 per cent. Extremely low temperatures are believed to limit the range of this species. Brood mortality varies with location, stage, and condition of the brood. Winter killing has no lasting effect upon epidemic trends. Weather station records furnish a fairly satisfactory basis for estimating the amount of winter kill.

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INTRODUCTION

The importance of temperature as a limiting factor in the distribution and seasonal abundance of insect species has long been recognized. Each species, through adaptation, has become adjusted to life within the range of temperatures prevalent in its natural habitat. Even so, temperatures may occasionally occur that are fatal to part of an insect population. Mortality of an insect pest, as the result of critical temperatures, may influence its seasonal abundance and hence be an important consideration in deciding the necessity of adopting artificial control measures. Recent subzero temperatures in the ponderosa pine region of the Pacific Northwest have given an opportunity to determine the lower critical temperatures for one of our most destructive tree-killing bark beetles, the western pine beetle, Dendroctonus brevicomis Lec.

The western pine beetle is a transition zone species inhabiting the Pacific Coast portion of the range of ponderosa pine from Lower California to British Columbia, and eastward into Idaho and Montana. In this area it is normally subjected to air temperatures of from -10 degrees F. to 105 degrees F. Since critical temperatures for this 2 beetle lie below 5 degrees F. and above 105 degrees F., it is apparent that the species, being protected to some extent by insulating layers of bark, is well adjusted to the usual temperatures in its geographic range.

D.b. beetles succumb in temperatures above 95° F when subjected to these temperatures for periods of one hour or less. JEG

In certain parts of its normal range, from time to time, abnormally low temperatures occur which are fatal to part of the overwintering broods. On the western slopes of the Sierra Nevadas and in the southern portion of its range, subzero temperatures sufficiently low to cause western pine beetle mortality rarely occur, but on the eastern slopes of the Sierra Nevadas and Cascades and in the northern part of its range, such temperatures are more frequent. In central Oregon, which is typical of the entire area covered in the present study, there is appreciable winter killing of western pine beetle broods about once in three years, and severe killing perhaps once in ten years. These killing temperatures cause a temporary reduction of western pine beetle population which, in certain instances, is reflected in decreased infestation during the season subsequent to the low temperatures. Temperatures within its normal range do not fall sufficiently low to exterminate the beetle population, and infestations soon resume their normal course, which is primarily influenced by factors other than climate.

The northeastern distribution of the species is apparently limited by the climatic zone in which temperatures of -20 degrees F. or lower are of annual occurrence. This is evidenced by the fact that the host plant, ponderosa pine, extends far beyond the eastern limits of western pine beetle occurrence, yet there is no insurmountable barrier, other than climate, to the eastward dispersal of the insect. Figure 1 shows the known distribution of D. brevicomis and its close relative D. barberi in relation to annual minimum temperature isotherms of -10 degrees F. and -20 degrees F.

Following three recent periods of subzero temperatures in eastern Oregon and northeastern California, extensive field examinations and detailed observations have been made to determine (1) the immediate effects of low temperatures upon overwintering western pine beetle broods, as measured by the amount of mortality soon after the low temperatures occur; (2) the influence of various factors upon the amount of mortality; (3) the net effect of low temperatures in reducing overwintering broods, as measured by the amount of emergence in the spring following periods of cold weather; and (4) the effects of reduced beetle population upon subsequent generations and the general trend of beetle outbreaks. The present paper summarizes the results of these examinations and observational studies and indicates to what extent this information may have practical value in connection with the conduct of control projects.

The study has been made possible only through the cooperation of several different agencies and many different individuals. We owe particular thanks to the ECW personnel, without whose funds and services the study could not have been carried on at all. Members of the Forest Service and Indian Service were very helpful during the winter of 1932-33 in collecting bark samples from many different areas, some of which were reached only under the most difficult conditions, and required back-packing of bark over many miles of deep snow. We have drawn heavily upon Bureau of Entomology and Plant Quarantine office reports by J. A. Beal and K. A. Salman, to whom credit for much of the original work is due. Other members of this Bureau who have aided at some time in the study are: W. J. Buckhorn, J. M. Whiteside, P. C. Johnson, P. N. Bacon, and H. W. Rohlotz. Mr. J. M. Miller, who has given a great deal of study to temperature effects under laboratory conditions, has been very helpful with information and suggestions.

HABITS OF THE WESTERN PINE BEETLE

The habits of the western pine beetle, particularly those of the overwintering brood stages, have an important bearing upon its resistance to low temperatures, so it is necessary to briefly review certain habits of these beetles.

Female beetles lay eggs along galleries constructed in the phloem, or inner bark. The larvae, upon hatching, mine for a time in the phloem, then most of them migrate outward into the corky bark where transformation into the pupal and adult stages takes place. For a more complete discussion of the life history and habits of this insect, see Hopkins (5).

Unpublished studies by Salman show that the first instar larvae confine their activity to the inner bark. The second instar larvae live both in the phloem and the outer bark, but still near the phloem. The third and fourth instar larvae, for the most part, mine in the outer bark. For convenience in the present temperature study, the larvae have been divided into two groups: small larvae, first and second instar; and large larvae, third and fourth instar. These terms are somewhat misleading in that size is not always a true criterion of the larval instar. More exactly, the division is one of difference in habit, for the small larvae feed primarily in or very near the phloem, whereas most of the large larvae live in the outer bark.

Usually, if not always, a majority of the brood overwinter as large larvae, but an appreciable number of eggs and small larvae may be found. Young adults[1] and parent adults comprise a very small and relatively unimportant portion of the total overwintering brood.

[1] Young adults are considered to be those newly formed individuals that have not emerged from the trees in which they developed, as contrasted with the parent adults which have emerged, attacked and established a progeny.

In the winters of 1932-33 and 1935-36, large larvae were found to predominate as usual. This was determined by data from sample plots, and a large number of bark samples from infested trees. While the proportion of different brood stages varies somewhat on different areas and in the different years, data taken from 393 samples from 2 percent of the infested trees on a large control project in Modoc County, California, during the winter of 1932-33, show the general relationship. (Table 1).

Table 1

Overwintering *D. brevicomis* Brood Stages
Winter of 1932-33
Modoc County, California

Eggs	Small Larvae	Large Larvae	Young Adults
1.5%	26.8%	71.1%	.6%

In the light of general observations, it is believed that the percent of large larvae shown in the above table may be somewhat too conservative.

NORMAL MORTALITY

For the western pine beetle, as for any insect species, there is a more or less constant death rate during the developmental period. This may be termed the normal or usual mortality, and must be determined before the abnormal mortality can be recognized as such.

Population counts at different stages of western pine beetle development, which were made over a period of eleven years in the same general region to which our winter mortality records apply, have been summarized in an unpublished report by Keen. These counts show that an average of 432 eggs are laid to each square foot of infested bark; 346 larvae hatch; 200 reach the full grown larval stage; and but 63 adult progeny emerge from the bark. Thus, the normal hazards of life for the western pine beetle, under all conditions from the egg to the adult stage, cause a reduction of about 85 percent. That most of this mortality occurs during transformations and little during a given stadium was found by Beal in laboratory studies of brood development.

Even in winters when temperatures are not critically low, there are several months in which no transformations take place. During the quiescent winter period, brood mortality is usually not in excess of 5 percent when killing temperatures do not occur. This has been shown through the examination of several thousand square feet of bark containing overwintering brood of different stages and from many different areas during mild winters.

Eggs and small larvae which overwinter in the phloem, or very close thereto, appear to experience such altered conditions of food and environmental moisture that, upon resumption of activity in the spring, very few are able to complete their development. Caging studies by Buckhorn have shown that in mild winters, trees containing overwintering eggs and small larvae have produced only about 20 percent as much progeny as those with overwintering large larvae. Thus, the normal hazards for overwintering small larvae are much greater than for large larvae.

Abnormal mortality caused by low temperature, in contrast to normal mortality, is easily recognized. The dead larvae present a characteristic, leaden appearance, which can be duplicated by exposing healthy brood to low temperatures under controlled conditions. Accordingly, when excessively low temperatures have occurred in the field, it is possible to determine the presence or absence of winter killing by direct observations. By sampling the population soon after low temperatures occur, it is possible to measure rather accurately the immediate amount of brood reduction.

IMMEDIATE EFFECTS OF LOW TEMPERATURE

In the present study, the immediate effects of cold weather upon overwintering western pine beetles was determined through population counts made shortly after the cold weather of December 1932, February 1933, and November 1935. Samples of infested bark were obtained in the ponderosa pine stands east of the Sierra Nevada and Cascade ranges, from northern California to northern Washington. Most of these were from central and southern Oregon and northeastern California. All population counts were made by carefully shaving the samples of infested bark and noting all living and dead individuals. The dead were easily recognized during the first month or two following the low temperatures, but after that length of time they became increasingly difficult to see because of the disintegration of the larvae, more especially the small larvae. Because of limited personnel, it was impossible to make all of the counts within the desired time, so whatever errors were made in the counts tend to underestimate the effect of the low temperatures.

In all, 1,864 samples comprising 1,002 square feet of infested ponderosa pine bark, which contained 185,169 living or dead western pine beetles in different brood stages, were examined. It was found that 25 to 50 samples of from 100 to 200 larvae each would give a maximum error in the average mortality of not more than 10 percent, the exact number of samples depending upon how they were selected. Although no one series of samples gave a high degree of accuracy, it is believed that the large number of observations gives a fairly accurate basis for estimating the immediate effects of low temperatures upon overwintering western pine beetle broods. Two hundred fifty-three of the samples were examined to determine the exact position of the overwintering brood in the bark.

The fatal low temperatures which occurred in December 1932, were remarkable for their long duration, lasting from the 7th to the 17th. The coldest day was the 11th, when -38 degrees F. was recorded at Meacham, Oregon. A strong wind blew, more or less constantly, resulting in a thorough agitation of the air so that similar temperatures prevailed over wide areas.

Mortality of western pine beetle broods, determined by a large series of bark counts made immediately following this freeze, are shown in Table 2. Nearly as many more areas were represented in the sampling, but only those based on fairly adequate samples are included in the table. Killing was noted in Oregon and northeastern California, but there was very little in Washington, where temperatures were not so severe.

Cold weather in February 1933, was of much shorter duration, lasting only two to four days, but was of much greater intensity. An all time record of -54 degrees was established for the State of Oregon. The distribution of the low temperatures was somewhat different than that of the December freeze and caused additional western pine beetle mortality in Oregon and Washington, but little, if any, in California. There was also killing in a number of areas, particularly in Washington, that had not been affected by the December freeze. Brood mortalities following the combined December and February freezes are shown in Table 3.

Table 2

Mortality of _D. brevicomis_ Brood in Midwinter
Following Low Temperatures of December 1932

Area	Approximate Minimum Degrees F.	Number of Samples	Number of Square Feet of Infested Bark	Percent of Brood Mortality
Deschutes N. F.	-30	54	39.4	84.5
Deschutes N. F.	-33	40	17.4	82.7
Deschutes N. F.	-12	21	20.2	57.9
Klamath Indian Res.	-19	28	23.0	74.1
Ochoco N. F.	-21	164	114.2	56.1
Umatilla N. F.	-14	20	12.1	29.3
Klickitat Co., Wash.	- 3	17	15.8	9.2

Table 3

Mortality of *D. brevicomis* Brood in Midwinter
Following Low Temperatures of
December 1932 and February 1933

Area	Approximate Minimum Degrees F.	Number of Samples	Number of Square Feet of Infested Bark	Percent of Brood Mortality
Deschutes N. F.	-22	50	43.1	47.0
Deschutes N. F.	-22	30	18.5	46.1
Fremont N. F.	-26	13	7.3	76.6
Klamath Indian Res.	-25	37	52.3	87.6
Klamath Indian Res.	-26	20	10.2	75.0
Klamath Indian Res.	-26	20	9.0	68.0
Malheur N. F.	-35	46	22.6	87.3
Malheur N. F.	-44	86	54.6	81.3
Malheur N. F.	-44	65	32.7	86.8
Malheur N. F.	-44	53	22.5	84.6
Ochoco N. F.	-35	101	40.9	79.9
Ochoco N. F.	-26	41	18.6	53.0
Ochoco N. F.	-35	45	20.8	90.7
Rogue River N. F.	-10	47	31.5	33.6
Umatilla N. F.	-25	50	28.1	50.2
Whitman N. F.	-35	25	8.5	61.3
*Klickitat Co., Wash.	-13	16	13.0	40.6
*Wenatchee N. F.	-14	39	18.7	26.1

*Affected only by February 1933 freeze.

These mortality counts and other brood examinations showed some killing of western pine beetle broods in nearly all ponderosa pine forests east of the Sierra and Cascade ranges, from Lake Tahoe, in California, to northern Washington and presumably into Canada. The accompanying map, Figure 2, shows the approximate distribution of light and heavy mortality in ponderosa pine stands affected by these two periods of low temperature. Light killing, or that of less than 50 percent, occurred from the vicinity of Lake Tahoe to Modoc County, California; in small areas in Oregon, affected by the Klamath River and Columbia River climates; and in most of the State of Washington. Heavy killing, or that above 50 percent, occurred in Modoc and Siskiyou Counties, California; southern and central Oregon; and the northermost part of Washington.

Low temperatures occurring from the first to the fifth of November, 1935, although rather severe in a few localities, were chiefly notable for their unseasonable character. A new early season record of -27 degrees F. was established in Oregon. The brood mortalities following these unseasonable temperatures are shown in Table 4. As indicated on the accompanying map, Figure 3, the effect of this cold period was more or less limited to central and southern Oregon. Heavy killing was restricted to a relatively small area south and east of Bend, Oregon. ~~Little or no killing occurred in California or Washington.~~ Perceptable killing occurred in the Modoc area of northeastern California but there was little or none in the state of Washington.

Table 4

Brood Mortality of D. brevicomis in Late Fall
As a Result of Low Temperatures
in November 1935

Area	Approximate Minimum Degrees F.	Number of Samples	Number of Square Feet of Infested Bark	Percent of Brood Mortality
1. Klamath Co., Ore.	+ 2	49	23.9	6.8
2. Fremont N. F.	-13	44	25.9	38.8
3. Deschutes N. F.	-20	42	16.1	60.7
4. Deschutes N. F.	-20	42	18.2	56.8
5. Deschutes N. F.	-15	41	23.6	43.8
6. Ochoco N. F.	0	35	22.7	8.5

The records of minimum temperatures and corresponding brood mortalities for the three periods of cold weather, given in Tables 2 to 4, have been combined in graphic form, Figure 4, in order to show their general relationship. It is evident from this graph that, within rather broad limits, there is a definite relationship between minimum temperatures and brood mortality, but before any closer correlation can be shown, it will be necessary to evaluate some of the more important modifying factors. Even in its present form, this graph serves as a rule of thumb method whereby the approximate kill may be determined from any given air temperature. Its relative accuracy in this respect was tested by the November 1935 freeze. Six areas were sampled and the brood mortalities determined. These fell within 7 percent of the theoretical and did not depart from the average in any case more than did the mortalities of the 1932-33 freeze, which were used in constructing the curve.

It is fortunate that observations are available on the effects of these three periods of low temperatures, for they afford an opportunity to compare the effects of the three types of cold weather which would logically be expected to produce the greatest brood mortality: a period of prolonged cold; a period of intense cold; and a period of unseasonable cold. Comparing the effect upon brood mortality of these three different types of cold weather periods, we find that for similar minima there is very little difference in the amount of kill, at least not enough to be significant within the wide fluctuations found when relating brood mortality to local weather station temperatures. Table 5 gives the basis for this comparison.

Table 5

Brood Mortality According to Type of Cold Weather

Minimum Temperatures	Average Mortality (Percent)	Prolonged Cold December, 1932 (Mortality %)	Intense Cold February, 1933 (Mortality %)	Unseasonable Cold November, 1935 (Mortality %)
-12° F.	33	57.9		
-13	36		40.6	38.8
-14	38	29.3	26.1	
-15	40			43.8
-19	51	74.1		
-20	52			56.8
-20	52			60.7
-21	55	56.1		
-22	58		47.0	
-22	58		46.1	
Average Deviation		+10.1%	-7.5%	+5.0%

It appears from Table 5 that the prolonged cold is somewhat more effective than the other two types. Unseasonable cold also causes slightly higher mortality than the average; while a short period of intense cold is apparently not quite as effective as the other two.

The difference between the prolonged period and the short one is quite likely merely a difference in the actual temperatures which are produced under the bark. The greater effectiveness of unseasonable cold is probably more due to brood conditions than to temperature factors.

In the 1932-33 freeze, slight regional differences in cold resistance were also noted. A higher mortality (65 percent at -19 degrees F.) was found on the Modoc, California, area than occurred at similar temperatures further north. This may indicate a difference in regional strains of beetles or merely a difference in method of sampling.

MODIFYING FACTORS

The effect of low temperatures upon western pine beetle broods under field conditions depends upon several important factors, particularly the temperatures to which broods are exposed, the environmental conditions surrounding them, and the condition of the broods. Since each of these factors is influenced by several variables, there is a complex relationship to consider in determining the amount of mortality that results from a given air temperature. In studying the effects of recent low temperatures, these variables have been given special consideration in order to evaluate the importance of each.

Temperatures

The lack of a close degree of correlation between air temperatures and brood mortality, as indicated in Figure 4, is undoubtedly due in large measure to the fact that weather station air temperature records do not apply closely to local forest conditions. Only a few of the low temperature records of the three cold periods were taken in ponderosa pine stands. Usually the weather stations were in communities located in open valleys where minimum temperatures dropped somewhat lower than in nearby forests. The differences were greatest during still, cold, clear nights at the very time when the extreme minima occurred. Therefore, it is difficult to determine what actual temperatures prevailed over the varied topography from which bark samples were taken, but for lack of better information, the weather station records had to be used even though they applied only approximately.

Subcortical temperatures to which broods are actually exposed depend upon the air temperatures in the forested area modified by the insulating properties of the bark. Beal (3) has shown, from studies in central Oregon, that there is a definite relationship between air and bark temperatures. During cold weather, subcortical temperatures do not fall as low as those of the air, the differences being governed chiefly by bark thickness and the rate of temperature change. Not only is there a difference of as much as 29 degrees F. between air and subcortical temperatures in bark of varying thickness, but there is a lag of from one to two hours in the reaction of bark temperatures to air temperature changes.

Since bark thickness plays such an important part in modifying subcortical temperatures, it is of interest to know the proportion of bark of various thicknesses which is normally found on infested ponderosa pines in forests of this region. Fortunately, it is possible to determine this by a series of calculations from available data. The typical distribution of bark thickness classes for all infested ponderosa pines on average site IV[2] stands in Oregon and Washington is

[2] A classification used by foresters to designate stands reaching an ultimate average height of between 4.6 and 6.5 logs of 16 feet each.

shown in Table 6. These percentages apply fairly well to all stands in which mortality records have been taken in this study.

Table 6

Amount of Infested Bark of Various Thicknesses
Site IV - Ponderosa Pine, Oregon

Bark Thickness (Inches)	Percent of Total Bark Surface
1/2 or less	.9%
5/8 to 1	67.0
1-1/8 to 1-1/2	27.7
1-5/8 to 2	3.6
2-1/8 and over	.8

It will be noted that only a very small percentage of bark is less than 1/2 inch in thickness or more than 2 inches; and nearly 95 percent of all bark is from 5/8 to 1-1/2 inches in thickness. Therefore, what happens to broods in bark of from 5/8 to 1-1/2 inches thick is of the greatest consequence in determining the total results of cold weather in any area.

Since the amount of insulation which the bark affords is directly dependent upon the amount of bark covering the brood, exact measurements were made in the winter of 1935 of the position of 19,885 large larvae in bark of varying thicknesses. The average amount of insulating bark over large larvae in each bark thickness group is shown in Table 7. The protective bark covering over eggs and small larvae was calculated from 10,162 of these measurements, where large larvae lay adjacent to the phloem, by adding 1/8 inch for phloem thickness. By multiplying the percent occurrence of brood in each bark thickness group by the relative abundance of that bark thickness group on all infested trees (from Table 6), weighted averages were determined which show the relative amount of insulating bark over all immature stages under field conditions. These calculations show that in central Oregon, approximately 95 percent of the overwintering brood are protected by one inch or less of bark. (Table 7).

Table 7

Amount of Insulating Bark over Eggs and Larvae
of D. brevicomis in Midwinter
Oregon, 1935

Bark Thickness Group	Percent of Total Brood by Insulation Groups												Number of Individuals
	1/4"	1/2"	3/4"	1"	1-1/4"	1-1/2"	1-3/4"	2"	2-1/4"	2-1/2"	2-3/4"	3"	
1" or less	29.3	48.9	20.2	1.6									2,829
1-1/8" to 1-1/2"	24.0	27.0	27.4	16.9	4.2	.5							9,547
1-5/8" to 2"	18.4	16.6	15.8	20.8	14.7	8.3	5.1	.3					4,801
2-1/8" and over	12.2	12.3	10.6	12.8	11.1	15.9	12.1	9.8	2.0	.5	.6	.1	2,708
	Weighted Averages, Large Larvae												
All Bark Thicknesses	27.3	41.4	22.0	6.6	1.8	.6	.2	.1					19,885
	Weighted Averages, Eggs and Small Larvae												
All Bark Thicknesses	9.4	33.2	39.4	12.6	3.7	1.1	.4	.1	.1				10,162

Since the amount of insulating bark covering overwintering broods is known, and since Beal (193~~4~~3) has determined the relation between air and bark temperatures, it is possible to estimate the temperatures to which various proportions of the brood will be subjected at any given air temperature. As an example, Table 8 shows the minimum temperatures to which various proportions of brood are subjected when the minimum air temperature drops to -26 degrees F. Two features stand out; first, that over 95 percent of the brood has one inch or less of insulating bark covering which gives a protection of from 8 to 21 degrees; and second, that a high degree of protection is given to a small percent of the brood protected by thick bark. This latter, no doubt, is one of the factors contributing to the continuation of the species in those parts of its range where extremely low temperatures are common.

Table 8

Proportion of Overwintering D. *brevicomis* Broods
Subjected to Various Subcortical Temperatures,
Given a Minimum Air Temperature of -26° F.

Thickness of Insulating Bark	Percent of Total Number of Large Larvae	Percent of Total Number of Eggs and Small Larvae	Spread Between Air and Bark Temperatures	Temperatures to Which Brood is Subjected	Lag of Bark Temperature Behind Air Temperature
1/2" or less	68.7	42.6	8°	-18°	1 hour
5/8" to 1"	28.6	52.0	18° to 21°	-5° to -8°	1 hour
1-1/8" to 1-1/2"	2.4	4.8	22° to 27°	+1° to -4°	2 hours
1-5/8" to 2"	.3	.5	26° to 29°	+3° to 0°	2 hours
2-1/8" and over	.0	.1	No data	No data	No data

That this protection afforded by insulating layers of bark is also reflected in a reduction of brood mortality following low temperatures has been shown in all of the studies made so far. In general, brood mortality, as stated by Miller (7) and Beal (3), varies inversely as the thickness of the bark in which the brood overwinters - i. e., the thicker the bark the less the mortality.

Total bark thickness, however, is only a rough measure of the amount of insulating bark over the brood. In order to evaluate the effect of insulation more exactly, the mortality percentages among 19,885 large larvae, previously referred to, have been arranged in graph form, Figure 5-8, in relation to the amount of insulating bark over the brood. This shows a general decrease in mortality with an increase in insulation, except for insulation of less than 1/4 inch. Mortality for brood with the least amount of insulation, 1/4 inch, falls decidedly and consistently out of line in all of the four areas sampled. This indicates, apparently, that some factor other than the amount of insulation is effective in reducing the amount of winter kill for the more exposed larvae. No ready explanation occurs to account for this exceptional condition.

Environmental Factors

Analysis of bark samples subsequent to the 1932-33 low temperatures showed an important variation in the proportion of brood mortality according to the height on the tree. On four areas, trees were felled and sampled at intervals along the trunk. The average mortality, as shown by basal samples alone, was found to be from 15 to 20 percent less than when the entire tree was sampled. (See Table 9). Even when bark of the same thickness was compared, it was found that mortality would be practically uniform in the upper portion of the trunk but considerably greater than that at the base (5 to 20 feet above the ground). The reason for this is not well understood but may be due to a real difference in temperatures, with colder air in the tree tops, due to increased radiation from the crowns, than close to the ground; or it may be due to a difference in bark character or brood condition.

Brood mortality is consistently greater on the north than on the south side of infested trees, following periods of very cold weather. This is well illustrated by a statistical analysis of the difference of mortality on the north and south sides of 145 trees sampled in the winter of 1932-33. In this comparison, mortality on the north was found to be 30 percent greater than that on the south side, and, since the standard error of sampling was only 4 percent, the difference is certainly significant.

Table 9

Average Mortality of Western Pine Beetle
in Total and Basal Bark, All Thicknesses
Oregon, 1932-33

Area	Percent Mortality (Total Bark)	Percent Mortality (Basal Bark)	Percent Mortality (Difference)
Ochoco Nat'l Forest	53.0	29.5	23.5
Klamath Indian Reservation	84.2	69.4	14.8
Deschutes N. F., Area 1	81.0	63.0	18.0
Deschutes N. F., Area 2	74.6	52.2	22.4
TOTAL AVERAGE			19.7

The higher mortality on the north side was despite the fact that the bark was on the average one-eighth of an inch thicker than on the south side. (This difference in bark thickness appears to be characteristic of ponderosa pine and is probably the result of greater weathering on the south side.) Two possible reasons may account for the higher mortality on the north side. Minimum temperatures reach about the same level on both sides, but on bright days temperatures do not rise as rapidly or as much on the north as on the south side; therefore, the duration of cold is much longer on the north. The second consideration is that because of generally colder conditions on the north side, brood does not develop as rapidly as on the south side. Overwintering larvae are smaller, the bark is tighter and more moist. As will be shown later, these conditions have a pronounced effect on increasing mortality.

In all series of samples that have been taken to determine brood mortality, there has been an observed difference in mortality in bark of different character. A much higher survival has been repeatedly noted in soft, spongy bark as contrasted with hard, flinty bark. This can hardly be explained as due to a difference in insulating properties, since the diffusivity, upon which insulation depends, is practically the same for all ponderosa pine bark. It seems most likely that the visible differences in bark character reflect certain differences of moisture content and available food for bark beetle development. These factors would have an important bearing upon the physiological resistance of individual larvae to low temperatures, which in turn would be reflected in different mortality rates.

That there is a definite relationship between amount of mortality and nearness of brood to the inner bark was noted following the freezes of 1932-33, and 1935. In general, brood closer to the inner bark showed higher mortality, in spite of the fact that this usually involved more insulation. It was of interest, therefore, to determine where the bulk of overwintering brood was located with reference to the inner bark and the importance of this factor in determining mortality.

Small larvae, as has been pointed out, confine their activity to the moisture-laden, highly nutritious phloem region. Exact measurements of the position of 19,885 large larvae, in the samples already referred to, showed that 99 percent of the overwintering large larvae occur within 3/8 inch of the inner bark surface. Of these, 23.7 percent are in contact with, but rarely within, the phloem. (See Table 10.)

The relative mortality of brood in relation to proximity to the inner bark surface was determined following the low temperatures of November, 1935. This relationship for bark of all thicknesses is shown in Figure 5-A. The basis for this graph is the same as for Figure 5-B, except that the measurements were taken to the inner bark surface instead of to the outer surface. A straight relationship is quite evident in that mortality decreases rapidly with increased distance from the inner bark.

Table 10

Position of D. *brevicomis* Overwintering Large Larvae
in Relation to the Inner Bark Surface
Oregon, 1935

Bark Thickness Group	Percent of Total Brood by Distance from Inner Bark Surface								Number of Larvae
	Phloem	1/8"	1/4"	3/8"	1/2"	5/8"	3/4"	7/8"	
1" or less	25.9	60.3	12.1	1.4	.3				2,829
1-1/8" to 1-1/2"	19.7	52.2	21.0	5.0	1.5	.4	.2		9,547
1-5/8" to 2"	15.2	50.0	22.7	7.1	3.7	.9	.4		4,801
2-1/8" and over	11.3	44.5	27.6	9.1	4.9	1.5	.7	.4	2,708
Weighted Averages	23.7	57.5	15.1	2.7	.8	.1	.1		19,885

Larvae living in the phloem region have the greatest amount of insulation, yet the mortality of this group was decidedly higher than that of the larvae living farther out in the bark. Therefore, larvae near the phloem must succumb to higher temperatures than those in the outer bark, for the insulating effect of bark thickness has already been demonstrated. It is interesting to note that in thick bark the larvae tend to occur in the phloem much less frequently than in thin bark (see Table 10), which might partially account for the lower mortality to brood in thick bark.

During the examination of samples, it was recognized that large larvae tend to be distributed in the bark in two characteristic patterns. In one type the brood is concentrated in or very close to the phloem, and, more often than not, these larvae are smaller than average in size. Brood mortality is high in samples of this kind. In the second type, brood occurs in scattered fashion, but is chiefly well removed from the phloem. In samples of the latter type, larvae are of normal development and the relative mortality is low. Insufficient samples were available for statistical analysis of these tendencies, but from general observation the differences appeared to be quite marked.

That there is considerable difference between inner and outer ponderosa pine bark, both as to moisture and nutrient content, has been demonstrated in previous experiments. Jeffrey, in unpublished studies, found that food in the form of sugars is more abundant in the phloem than in the outer bark. It is altogether likely that the physiological condition of larvae feeding upon different types of food in the inner and outer bark would be affected and result in a corresponding difference in their reaction to low temperatures. Beal (~~5~~ 2) found that the phloem of southern pine contained 200 percent moisture and the outer bark only about 30 percent on a dry weight basis. He also found that the phloem moisture content of green ponderosa pine ranges from 163 percent to 214 percent, which approaches that of southern pine. The moisture content of the outer bark would undoubtedly be quite similar in both ~~instances~~ trees, for it would be in equilibrium with the moisture content of the air.

Miller (6) and Beal (1), (2) have shown that environmental moisture plays an important role in determining the resistance of Dendroctonus broods to low temperatures. Miller found that D. brevicomis larvae in saturated bark succumb to temperatures 10 degrees higher than do larvae from normal bark. Since moisture is such an important factor influencing brood resistance, it is not surprising to find that those larvae living closest to the inner bark surface suffer the highest mortality.

Cerambycid work (chiefly by <u>Acanthocinus spectabilis</u> Lec.), which tends to dry out the bark and decrease its moisture content, was observed to be associated with relatively lower mortality from freezing than samples having no cerambycid work. Considerable variation existed among the samples, however, so that conclusions based on statistical analysis were not possible.

<u>Brood Conditions</u>

Investigations in Oregon during the winters of 1932-33 and 1935-36 point to the conclusion that small larvae are less resistant to low temperatures than are large larvae. Miller (7) reported the reverse to be the case in California during 1932-33, although subsequent examinations showed that practically no brood developed from those trees containing small larvae at the time the low temperatures occurred.

Variations in larval size are closely associated with differences in environmental moisture and kind or condition of the food, which differences have been considered to be responsible for differences in cold hardiness. As has been pointed out, the small larvae live in or near the phloem, while most of the large larvae are in the outer corky bark. Proximity to the inner bark surface has been shown to increase the amount of brood mortality, so it is logical that mortality at a given temperature is greater among small larvae than among large larvae, (see Table 11).

Small larvae are not subjected to temperatures quite as low as are large larvae because of a greater amount of insulating bark. This increased protective covering over small larvae, to all practical purposes amounts to about 1/4 inch more of bark, which would make a temperature difference of approximately 4 degrees, (see Table 8).

Table 11

Percent Mortality of Small Larvae in the Phloem
as Compared to Average Mortality
of all Larvae From the Same Areas and Bark
of the Same Thickness
Oregon, 1932-33

Average Mortality All Larvae	Mortality of Small Larvae	Increased Mortality Among Small Larvae
38.7 %	100.0 %	158.5 %
74.5	100.0	34.2
32.9	88.0	167.5
32.9	100.0	204.0
16.5	100.0	505.0
16.5	43.7	165.0
40.8	100.0	145.0
72.7	100.0	37.5
72.7	100.0	37.5
72.7	100.0	37.5
72.9	96.4	32.6
54.7	100.0	82.9
54.7	100.0	82.9
		130.0 %

For some time it has been recognized that there is runting of larvae in certain trees, probably caused by adverse conditions of an undetermined nature within the bark. In examining bark samples to determine mortality, especially in the winter of 1935-36, it was evident time and again that samples containing small individuals, but undoubtedly in the third and fourth instars, would exhibit a much higher degree of mortality than those samples containing brood of normal size. This tendency has also been noted in laboratory studies at Berkeley.

Bark tightness is dependent very largely upon the degree of brood development; in general, the younger the brood, the tighter the bark. Since trees with tight bark contain the younger brood stages, it follows that brood mortality in these trees is higher than in those trees with loose bark. Observations in Oregon have supported this conclusion.

SUBSEQUENT EFFECT OF WINTER KILLING

The ultimate emergence of overwintering western pine beetle broods following the cold winter of 1932-33 was determined by emergence counts. These have been used for many years as a method of sampling *D. brevicomis* populations, since the emergence holes of the progeny can be distinguished from the entrance holes, ventilation holes and emergence holes of the parents. The emergence holes of the progeny are characterized by not connecting directly with the egg galleries as do the other types. While it has been found that approximately 1-1/4 beetles emerge per hole, the number of holes does give an index of the relative abundance of emerging populations.

During the summer of 1933, emergence counts of 3,500 square feet of bark was taken on some of the same areas where brood mortality counts had been made during the winter. For uniformity, samples were taken as follows: (1) from trees 16 to 30 inches in diameter at breast height; (2) from 15 to 25 feet above ground; (3) in bands around the trees so that all sides were equally represented; (4) to include normal attacks only; (5) to include bark only of average thickness. Under these conditions of sampling, it was found that from 15 to 20 square-foot samples from each of as many trees were sufficient to insure a maximum error in the average of not more than 10 percent. This method of sampling was applied to six areas in Oregon where over 3,000 of the samples were taken.

Counts in central and southern Oregon showed that the emergence in the spring of 1933 was less than 20 percent of that normally occurring following mild winters in the same area, (see Table 12). Approximately the same amount of reduction was noted in northern California, although the basis for estimates was not the same as in Oregon. No estimate was made of spring emergence in areas where there had been light winter mortality.

Supplementing the emergence counts, emergence from 165 square feet of infested bark on 29 ponderosa pines, which were subjected to low temperatures, was determined in the spring of 1933 by caging portions of the infested trees. This was done in central Oregon and northern California. The screen type of cage used in this work has been described and illustrated by Buckhorn (~~1936~~ 1934). These caging experiments showed that, while the average emergence was greatly reduced, a considerable residue of living beetles remained in the bases of some trees. These living beetles, of which as many as 90 to 100 per square foot emerged from some trees, were to be found only in the basal 10 feet of certain infested trees, mainly those with thick bark.

Table 12

Effects of Low Temperatures Upon Western Pine Beetle Population Winter of 1932-1933

Forested Area	Brood per Square Foot of Infested Bark		Brood Killed in Midwinter (Percent)	Reduction for Normal* Emergence (Percent)	Reduction in Volume of Timber Losses 1932 to 1933 (Percent)
	Living Larvae Following Freeze	Emergence in Spring, 1933			
Malheur N. F.	61	3	83	97	57
Bly Area	14	11	83	90	75
Fremont N. F.	65	5	81	95	61
Modoc N. F.	103	--**	65	--**	33
Ochoco N. F.	83	21	57	81	60
Deschutes N. F.	92	29	54	74	23
Lassen N. F.	164	--**	46	--**	9
Rogue River N. F.	143	21	33	81	50

* Normal emergence considered 112 beetles per square foot, based on emergence counts for mild winters of 1930 and 1931.

**No comparable data taken to show spring emergence.

SUBSEQUENT REINFESTATION

The after effects of the winter killing, as indicated by the amount of infestation which developed during the 1933 season, was determined through timber cruises of the amount of insect-killed ponderosa pine on 86 sample plots, totalling 24,180 acres. The plots, of 320 or 640 acres each, are located in California, Oregon and Washington. Many of them have been cruised annually for the last 15 years to determine the amount of insect-caused losses (primarily D. brevicomis). A comparison of the timber losses on these plots is the best available means of determining the status of infestation during any one year. The reduction of infested tree volume in 1933, on areas where considerable winter mortality occurred, is shown in Table 12. It is evident from ~~this~~ these data that the 1933 infestation was considerably less than that of 1932, but that this reduction was not always in proportion to the winter killing that had occurred.

EFFECTS UPON BENEFICIAL INSECTS

The effect of low temperatures upon the insect enemies of D. brevicomis is of importance in that they may suffer a greater amount of winter killing than their host. Not much information is available on this point, but the following observations have been made. Cerambycid larvae, mostly Acanthocinus spectabilis Lec., which destroy some western pine beetle brood by competing with them for space and food, are affected by low temperatures about the same as are the bark beetles. The clerid, Enoclerus lecontei Wolc., which is the most important insect enemy of the western pine beetle, is not so resistant to cold as its host. This is relatively unimportant, however, for most of the clerid larvae migrate to the base of the tree where they are protected from the low temperatures. The indications are, from general observations in the spring of 1933, that the clerid increases in relation to its host in seasons following low temperatures. The ostomatid, Temnochila virescens var. chlorodia Mann., which is a predator of some importance, is killed by about the same temperatures as E. lecontei, but since it does not migrate to the same extent suffers a higher mortality. T. virescens chlorodia was observed to be scarce in the spring of 1933.

CONTROL CONSIDERATIONS

The fact that low temperatures may cause widespread killing of western pine beetle broods immediately raises the question as to its importance in controlling outbreaks of this beetle. If low temperatures wipe out epidemics, there is little reason for spending large sums on control work. In order to determine the effects of winter killing upon epidemics, it is only necessary to observe the infestation trends in seasons following periods of low temperatures. For this purpose, there is much information available from annual cruises of timber losses on sample plots.

The record of western pine beetle infestation in southern Oregon since 1921 may be taken as an example. The fluctuations in volume[3] of timber killed per acre on 7,040 acres of plots cruised each year in the area between Klamath Falls and Lakeview, Oregon, is shown in Figure 6, together with the extreme minimum temperatures at a typical point in the area. Consideration of this graph shows that there has been no very noticeable effect of cold weather in halting beetle epidemics. The one exception appears to have been the very pronounced reduction in 1933, following the cold weather of the preceding winter. The effects of this cold apparently acted in the same direction as the infestation trend and served to accelerate the decline. ~~In general, it would seem that a rise of infestation is as likely to follow periods of cold weather as is a reduction.~~

[3] While the board foot timber volume losses on these plots are indicative of the relative abundance and economic importance of the western pine beetle from year to year, they must not be considered an absolute measure of the population. Several other insect species, including *Melanophila californica*, *Ips emarginatus*, *Ips oregoni*, and *Dendroctonus monticolae*, contribute to the seasonal losses on the plots, but killing by the western pine beetle constitutes the major part of the infestation -- more especially in years of epidemic losses. The entire problem of sampling the western pine beetle population is an important one, deserving of detailed consideration, which can not be given here.

In central Oregon cold weather is more frequent and more intense than in southern Oregon, which may explain why large areas of overmature ponderosa pine in just the right condition for beetle attack have escaped injury for so long a time. Unfortunately, no continuous record of the infestation in this area is available, but it is interesting to note that the first severe infestation of recent years occurred in 1931 and 1932, immediately following a period of very low temperatures in 1930, which were more severe in this particular area than those of 1932, which caused a brood reduction of from 50 to 85 percent.

The evidence so far would indicate that, in cases where a high percentage of brood is killed, this does have an effect in reducing subsequent infestation of the western pine beetle for a period of about one year, but anything less than a 50 percent kill of brood has little or no effect upon the general trend of western pine beetle epidemics. It is clear that even a severe reduction of brood by cold weather has no lasting effect upon epidemic trends and that these trends are primarily influenced by other factors.

Low temperatures, then, do not always alter the necessity for artificial control measures, but may influence them in certain years. A brood reduction by freezing of 50 percent or more is considered necessary to alter control work in the year of the low temperatures. To date, three control projects have been influenced by the effects of low temperatures upon western pine beetle broods. In 1932-33, control work on the Modoc National Forest, California, was stopped after it was partially completed, as a result of a 65 percent winter kill, Miller (7). The same winter a 50 percent freeze mortality resulted in the suspension of control work on the Cohoco National Forest, Oregon. In 1935, a proposed project on the Deschutes National Forest, Oregon, was abandoned because of a 50 to 60 percent winter kill of the western pine beetle. Three control projects during these two winters have been completed, although some winter killing occurred in the areas treated. In the spring of 1933 a small project was completed in the Warner Mountains, California, after a winter kill of 50 percent. This was a border line case which probably would have been abandoned, had it not been hoped to achieve a complete clean-up of infestation in a small area. In December, 1935, two projects were completed after a 30 to 50 percent winter kill in November of the same year. One of these projects was near Bly in southern Oregon and the other near Sisters on the Deschutes National Forest, Oregon.

The effectiveness of winter killing, like that of artificial control, depends upon an outright reduction of the beetle population without influencing the factors that tend toward an increase of the species. Therefore, if the underlying factors which govern the abundance of the insect are not altered in the meantime, it is necessary to maintain the temporary reduction of the population from year to year until the time when economic losses are slight or until the timber crop has been harvested. Winter killing, then, can be made use of in certain seasons to replace artificial control, but its effectiveness must be clearly recognized as being of short duration.

Since winter killing may at times replace artificial control, it is necessary to recognize when such killing occurs in order to take advantage of its help. This should present no great difficulty because winter killing of regional importance is caused only by widespread temperatures of -15 degrees F. or lower. Since in the range of western pine beetle such low temperatures are readily recognized by their unusual nature, there is little likelihood that their importance will be overlooked. From a study of the weather records, the general distribution and probable degree of winter killing may be estimated, since the approximate relation of air temperatures to mortality has been determined from this study, (see Figure ~~3~~ 4). Field investigations of the local effects of the low temperatures should then be made to verify these estimates.

SUMMARY

The western pine beetle, Dendroctonus brevicomis, a bark beetle destructive to ponderosa pine through its Pacific Coast range, is controlled to a large extent both in distribution and seasonal abundance by low winter temperatures. As a transition zone species, it is well adapted to the temperatures that normally occur in its range. Towards its southern limits there is no winter killing due to low temperatures, but from central California northward, winter killing occurs from time to time. Mortality from freezing increases toward the north to the point where the distribution of the species is limited by the isotherm beyond which temperatures of -20 degrees F., or colder, are of annual occurrence.

Normal mortality from the egg to adult stage is 85 percent, most of which takes place during transformations. Overwintering broods, which include mostly large larvae, a few small larvae, eggs and adults, suffer a normal mortality of about 5 percent during the hibernation period when no transformations occur. During extremely cold winters, killing of a large percentage of overwintering brood may take place. Sometimes this reduction of brood closely approximates 100 percent.

Three periods of cold weather have been investigated in this study: a period of prolonged cold in December, 1932; a period of intense cold in February, 1933; and a period of unseasonable cold in November, 1935. The combined cold of December, 1932, and February, 1933, caused some western pine beetle mortality in practically all ponderosa pine stands east of the Sierra Nevada and Cascade Ranges from central California to Canada. Mortality as a result of the November, 1935, cold weather was limited to central and southern Oregon. The data, although not conclusive, indicates that, given the same minimum temperatures, the prolonged cold was most effective, the unseasonable cold less effective, and the intense cold least effective in reducing western pine beetle populations.

Several factors influence the amount of brood mortality that will result at given air temperatures. These factors act by modifying the actual temperatures to which the broods are exposed, by change~~in~~ing environmental conditions, or by influencing the cold hardiness of individuals in the brood.

Bark thickness is of importance in modifying the subcortical temperatures to which brood is actually exposed. In general, mortality from freezing varies inversely as the thickness of the bark in which the brood occurs: that is, the thicker the bark, the less the mortality. The same relationship is evident when the amount of absolute insulation is considered, although the correlation is not good for insulation of less than one inch.

Winter killing at the base of trees averages 15 to 20 percent less than the general average for the entire tree. Above the base, the mortality rate is uniform for bark of the same thickness.

Winter killing decreases rapidly with increased distance from the inner bark -- that is, the farther the brood from the inner bark, the less the amount of mortality. This is a straight line relationship that gives a better correlation to mortality than does amount of insulation.

Small larvae are less resistant to low temperatures than are large larvae; brood in trees with tight bark is less resistant to freezing than brood in trees with loose bark; brood on the north side of a tree is less cold hardy than that on the south; abnormally small larvae succumb sooner than normal larvae; all probably for the same reason, for in each case the less resistant brood exists in or near the phloem where the amount of moisture is greater. Environmental moisture is known to be an important factor influencing cold hardiness.

Sampling in the spring of 1933 showed that the emerging population was less than 20 percent of that following mild winters. The residual population exhibited a decided tendency toward increase so that in some localities the 1933 infestation was nearly as great as that of 1932. However, for the entire area affected, the 1933 infestation was lower than in 1932, and considerably more so than it otherwise would have been, as indicated by the general infestation trend.

In general, the effects of low temperatures are not evident in the infestation trend except in extreme instances, about once in ten years, when the course of infestation may be altered for about one year. The cold weather of 1932-33 was an example of this kind. Anything less than 50 percent reduction has little or no effect upon the annual infestation; therefore, this amount of kill, or more, is necessary to influence artificial control projects. Three control projects have been affected by the effects of cold weather, two in 1932-33 and one in 1935-36.

The amount of winter killing can be estimated from minimum temperatures at standard weather stations with a fair degree of accuracy, depending upon how closely the weather station records apply to the forested area in question. Such estimates of amount of winter kill are of importance in determining the necessity for artificial control during winters having extremely low temperatures. It is usually necessary to check the accuracy of the estimates in the field before recommending modification of control work.

Cold weather affects the insect enemies of the western pine beetle to about the same degree as the host.

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FIGURE-1

DISTRIBUTION OF DENDROCTONUS BREVICOMIS AND D. BARBERI
IN RELATION TO AVERAGE ANNUAL MINIMUM TEMPERATURES

LEGEND

x - KNOWN DISTRIBUTION OF DENDROCTONUS BREVICOMIS

o - KNOWN DISTRIBUTION OF DENDROCTONUS BARBERI

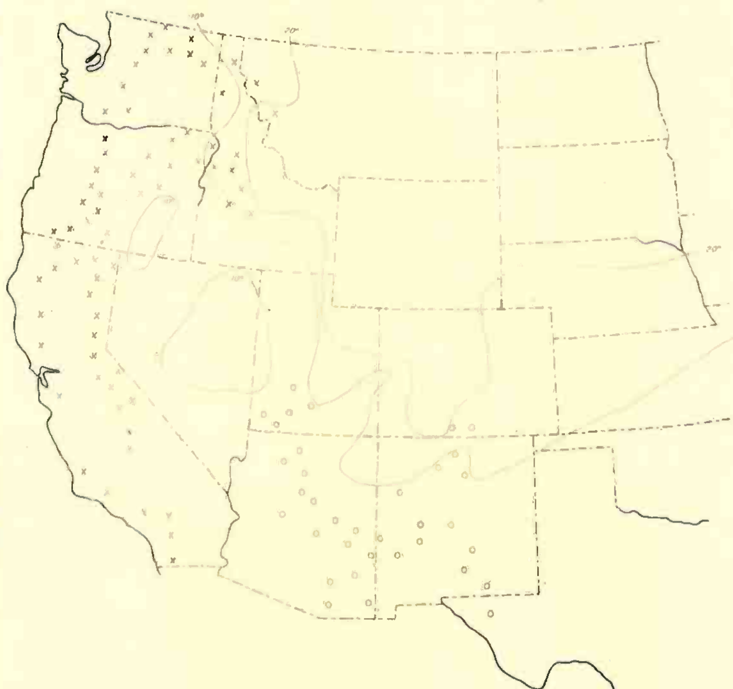


FIGURE-2

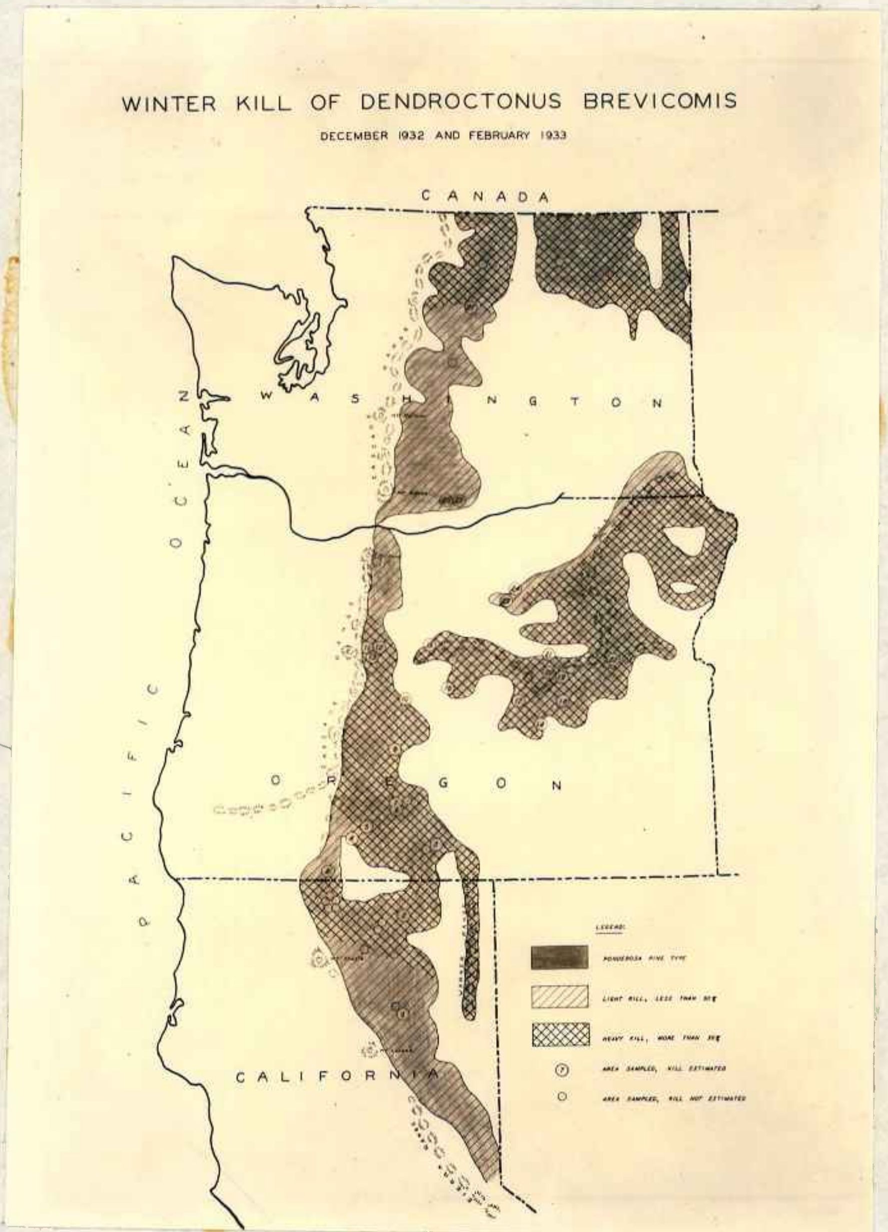

WINTER KILL OF DENDROCTONUS BREVICOMIS
DECEMBER 1932 AND FEBRUARY 1933
CANADA
WASHINGTON
OREGON
CALIFORNIA
PACIFIC OCEAN
LEGEND:
PONDEROSA PINE TYPE
LIGHT KILL, LESS THAN
HEAVY KILL, MORE THAN
AREA SAMPLED, KILL ESTIMATED
AREA SAMPLED, KILL NOT ESTIMATED

FIGURE-3

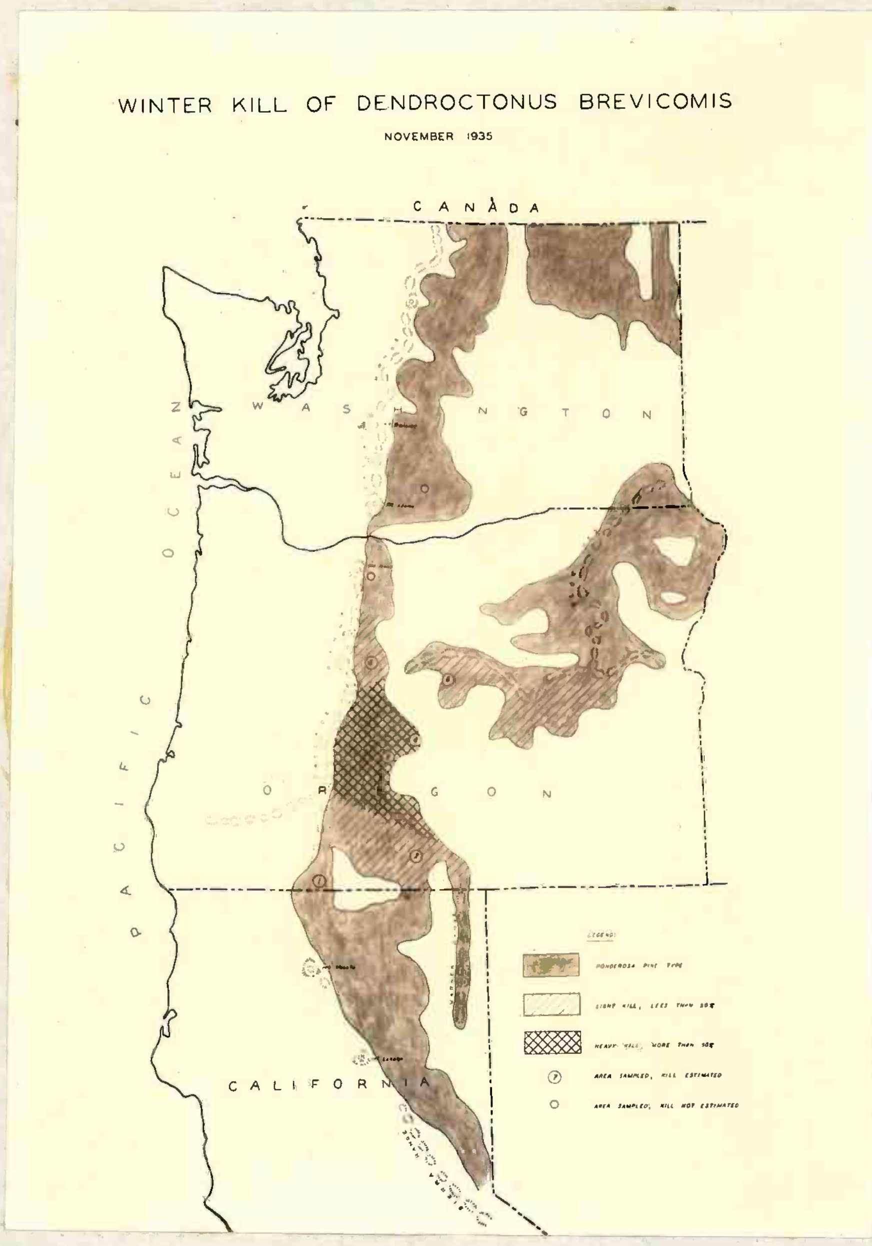

WINTER KILL OF DENDROCTONUS BREVICOMIS
NOVEMBER 1935
CANADA
WASHINGTON
PACIFIC OCEAN
OREGON
CALIFORNIA
LEGEND:
PONDEROSA PINE TYPE
LIGHT KILL, LESS THAN 50%
HEAVY KILL, MORE THAN 50%
AREA SAMPLED, KILL ESTIMATED
AREA SAMPLED, KILL NOT ESTIMATED

FIGURE-4

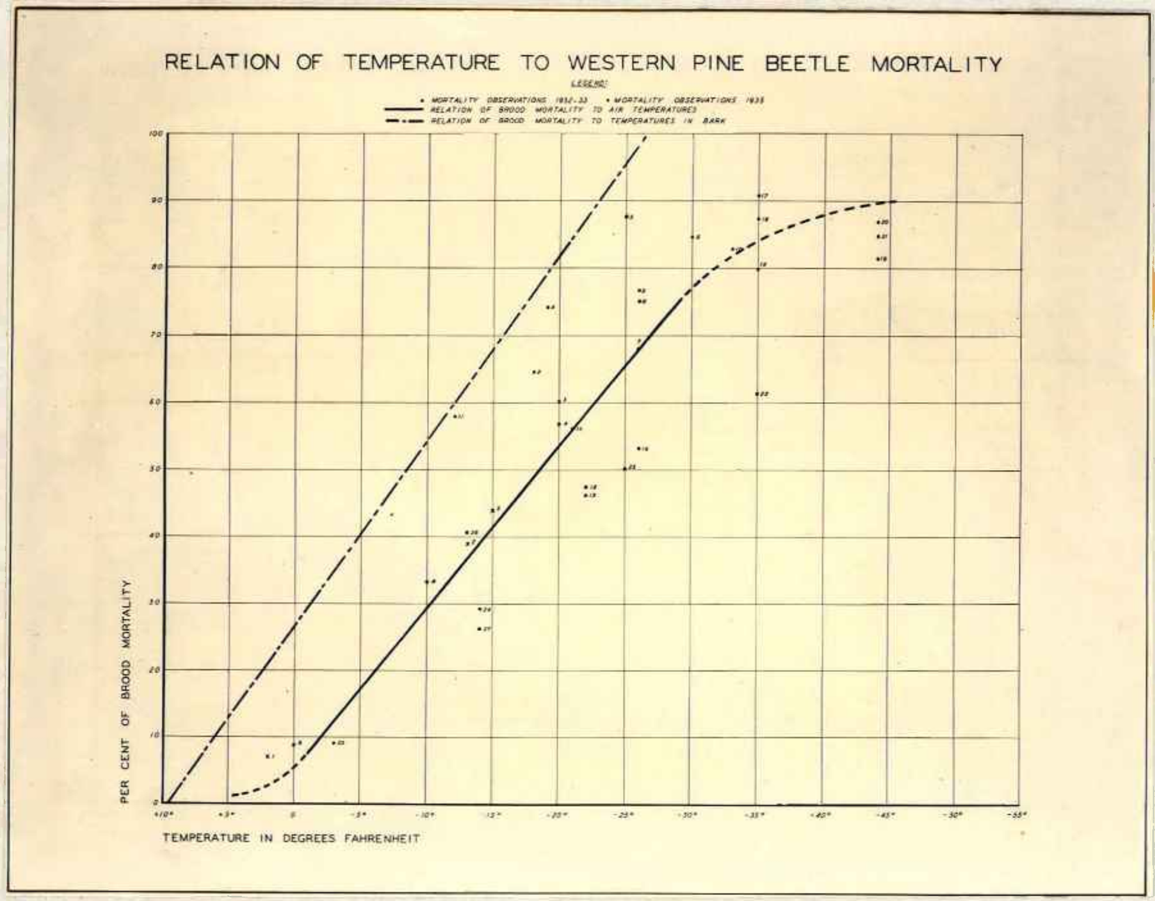
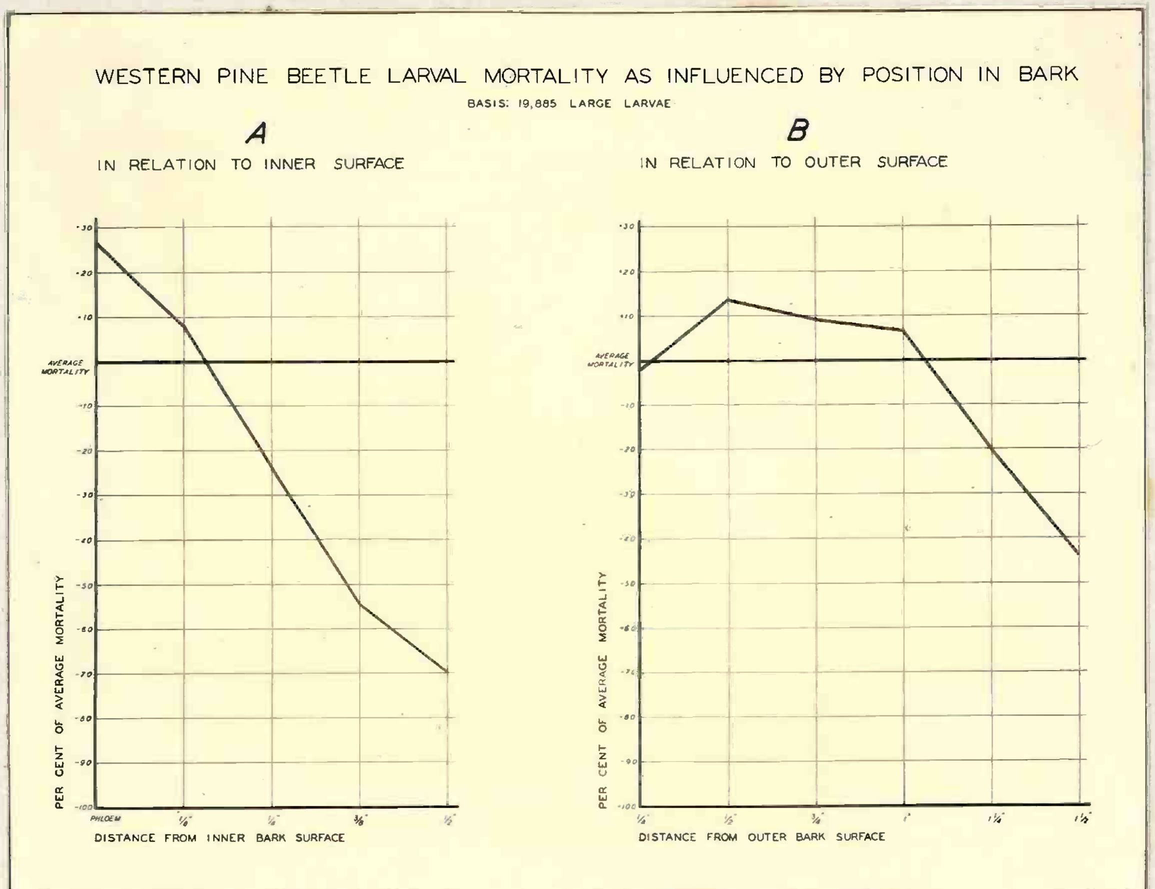
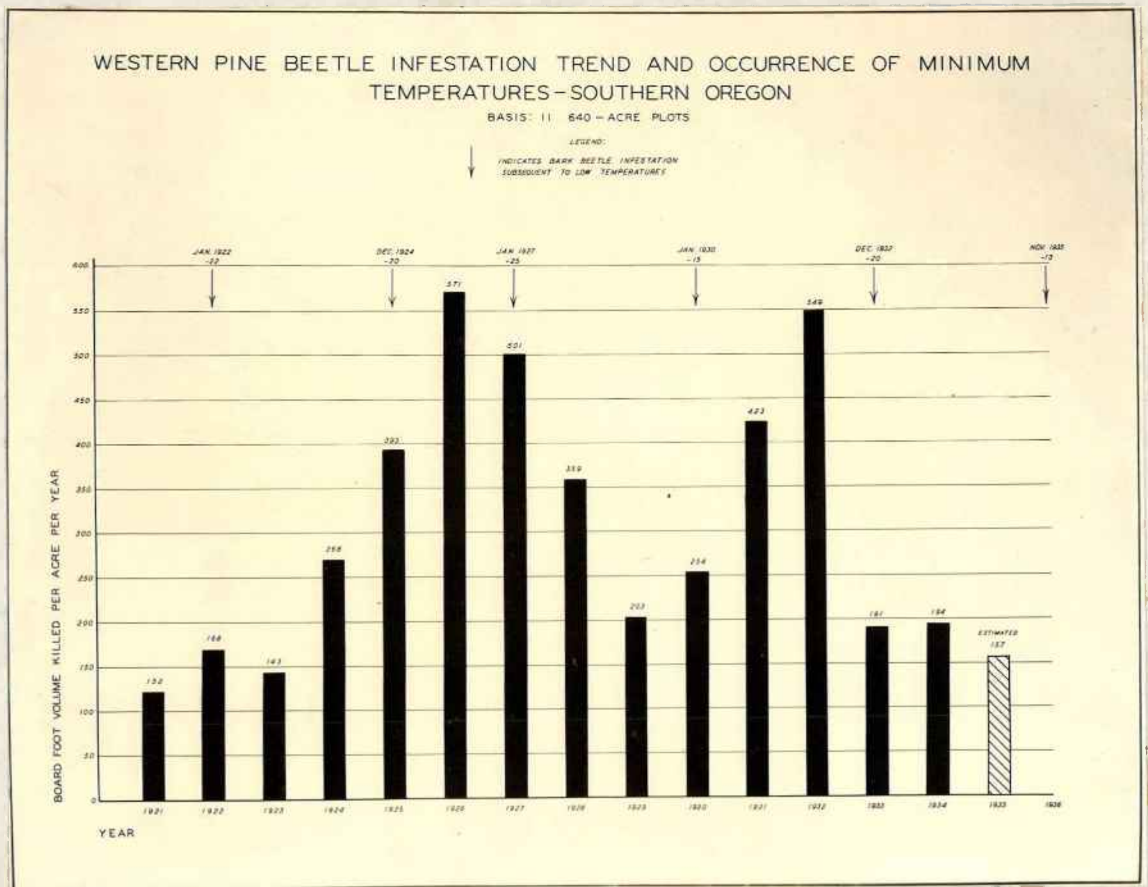

RELATION OF TEMPERATURE TO WESTERN PINE BEETLE MORTALITY
LEGEND:
MORTALITY OBSERVATIONS 1932-33
MORTALITY OBSERVATIONS 1935
RELATION OF BROOD MORTALITY TO AIR TEMPERATURES
RELATION OF BROOD MORTALITY TO TEMPERATURES IN BARK
PER CENT OF BROOD MORTALITY
TEMPERATURE IN DEGREES FAHRENHEIT

FIGURE-5



WESTERN PINE BEETLE LARVAL MORTALITY AS INFLUENCED BY POSITION IN BARK
BASIS: 19,885 LARGE LARVAE
A
IN RELATION TO INNER SURFACE
B
IN RELATION TO OUTER SURFACE
AVERAGE MORTALITY
PER CENT OF AVERAGE MORTALITY
DISTANCE FROM INNER BARK SURFACE
DISTANCE FROM OUTER BARK SURFACE
PHLOEM

FIGURE -6



WESTERN PINE BEETLE INFESTATION TREND AND OCCURRENCE OF MINIMUM TEMPERATURES - SOUTHERN OREGON
BASIS: 11 640 - ACRE PLOTS
LEGEND:
INDICATES BARK BEETLE INFESTATION SUBSEQUENT TO LOW TEMPERATURES
JAN. 1922 -22
DEC. 1924 -20
JAN. 1927 -25
JAN. 1930 -15
DEC. 1932 -20
571
501
549
132
168
143
258
203
254
181
194
ESTIMATED 157
BOARD FOOT VOLUME KILLED PER ACRE PER YEAR
YEAR